

Allee effect enhanced by fishing intensity in sedentary species fisheries and its bioeconomic consequences

Efecto Allee potenciado por la intensidad pesquera en pesquerías de especies sedentarias y sus consecuencias bioeconómicas

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Abstract

Understanding the low-density dynamics of marine sedentary species is an essential component for their sustainable management. When these stocks are subject to high levels of exploitation, Allee effects can be enhanced leading to recruitment failure, stock collapse, and the failure of enhancement and restoration programmes, even after fishing has stopped. In this study, we modelled the low-density depensation (Allee effect) of a generalized sedentary species under enhanced and unenhanced Allee effects and applied both scenarios to a fishery using a spatial bioeconomic model. The model was run under an open-access management regime to contrast the long-term implications under both scenarios. Under the enhanced Allee effect, the stock required a 70% increase in spawning stock density to maintain a probability of reproduction of 50% or higher, compared with the unenhanced scenario. The bioeconomic simulation showed that total biomass collapsed five years earlier in the enhanced scenario and lower performance among the principal bioeconomic indicators. We also identified a point of no return for the stock because of the Allee effect, beyond which the stock would not recover even when fishing was stopped. Management must aim to maintain spawning stocks above Allee threshold reference points and improve the understanding of the interaction between Allee effects and fishing effort, especially for stocks already reduced to low levels.

Key words: Allee effect; sedentary species; spatial model; depensation; stock recovery

Resumen

Comprender la dinámica poblacional de las especies marinas sedentarias en baja densidad es esencial para su manejo sostenible. Cuando estos *stocks* se exponen a altos niveles de explotación pesquera, el efecto Allee se puede magnificar, provocando fallas en el reclutamiento, colapso del *stock* y el fracaso de los programas de mejora y restauración, incluso después de que la pesca haya cesado. En este estudio se modeló la depensación a bajas densidades (efecto Allee) en una especie sedentaria bajo el efecto Allee potenciado por la pesca mediante un modelo bioeconómico. Se corrió el modelo bajo el esquema de manejo de acceso abierto para contrastar las implicaciones a largo plazo bajo dos escenarios: efecto Allee “natural” y efecto Allee potenciado por la pesca. Bajo el efecto Allee potenciado, el *stock* desovante requirió 70% de mayor densidad para mantener una probabilidad de reproducción de 50% o más, comparado con el efecto Allee no potenciado. La simulación mostró que la biomasa total colapsa cinco años antes en el escenario potenciado, con un rendimiento menor en los principales indicadores bioeconómicos. También se identificó un “punto de no retorno” para el *stock* como resultado del efecto Allee, más allá del cual el *stock* no se recobraría aun en ausencia de pesca. El manejo debe enfocarse en mantener un *stock* desovante por arriba del punto de referencia umbral Allee y mejorar la comprensión de la interacción entre el efecto Allee y el esfuerzo de pesca, especialmente para stocks que ya se encuentran en bajos niveles.

Palabras clave: efecto Allee, especies sedentarias, modelo espacial, depensación, recuperación del *stock*.

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Introduction

The understanding of low-density dynamics of marine sedentary or low-mobility species has been identified as a critical component of their management and conservation (Hilborn *et al.* 2014). Spatial heterogeneity and patchy distribution are typical of these species, many of which have evolved strong density-dependency related with social and reproductive functions (Stoner & Ray-Culp 2000). This density-dependency, therefore, has important implications for their reproductive fitness particularly when population density is reduced to very low levels either because of natural forces such as environmental catastrophes (Aalto *et al.* 2019), ecological forces such as predation (Gascoigne & Lipcius 2004b), or due to human exploitation (Stoner *et al.* 2012). The decrease in per-capita growth rate and the negative effect on reproductive fitness due to reduced density or abundance beyond a certain threshold is referred to as depensation (Liermann & Hilborn 2001). Among the most studied depensation mechanisms is the Allee effect defined as positive density-dependent effects on components of individual fitness (Liermann & Hilborn 2001). Allee effects are often associated with depensation properties that result in the reduced probability of reproductive success particularly difficulty in finding mates (Liermann & Hilborn 2001). The effect has been observed in several highly exploited sedentary marine species whose densities or abundances have reached relatively low levels, including sea urchins (Wing *et al.* 2003), gastropod mollusks (Stoner *et al.* 2012, Aalto *et al.* 2019), and sea cucumbers (González-Durán *et al.* 2018).

Reproduction in many sedentary species require proximity of mature adults to increase the probability of success. The level of density-dependency and subsequent proximity may therefore differ among species (Hilborn *et al.* 2014). Sea cucumbers and sea urchins, for example which release gametes to the water column for fertilization (Wing *et al.* 2003, Navarro & García-Sanz 2012), at a certain density or abundance may be considered less density-dependent relative to gastropod mollusks which have internal fertilization and require physical contact to mate (Stoner & Ray-Culp 2000). The intensity of depensation and Allee effects on these populations may therefore also differ given the specific spatial scale of the

environmental, biological, and exploitation profile of the populations considered (Hilborn *et al.* 2014).

Intensive human exploitation can cause rapid removal of the largest and most fecund individuals (Aalto *et al.* 2019), therefore resulting in enhanced Allee effects as populations are driven to low levels (Stoner *et al.* 2012). The implication is that populations are driven to densities where the probability of reproductive success is zero (the Allee threshold) (Liermann & Hilborn 2001) and are unlikely to recover to sustainable levels (Hilborn *et al.* 2014). This has been shown or speculated to be the case for simulated and empirical studies of sedentary populations including sea cucumbers (González-Durán *et al.* 2018) and queen conch (*Aliger gigas*) (Stoner & Appeldoorn 2021). The latter includes stocks that have undergone up to forty years of moratoria and stock enhancement measures and have yet to recover. When not considered in management, the Allee effect can therefore lead to stock collapses, local extinctions, socio-economic losses, and disruptions of ecosystems (González-Durán *et al.* 2018). Maintaining the integrity of spawning stocks are of principal importance towards the holistic management of sedentary species.

One of the approaches to incorporating the Allee effect is to model the relationship between reproductive success and the density of sexually mature individuals, subject to being reduced to low levels (Stoner *et al.* 2012, Hilborn *et al.* 2014). These models may be applied to populations from the local to mesoscale as depensation relationships may differ within subpopulations of the same species and among different locales with different exploitation and environmental conditions (Stoner *et al.* 2012).

In this study, we assess the bioeconomic impact of depensation intensity on a generalized sedentary species. Depensation or Allee effect intensity was defined based on the depensation parameter, a measure of the strength of the Allee effect on a population, from the depensation model of Hilborn *et al.* (2014). This depensation model was modified to include an offset to the right to define the Allee threshold density below which the probability of reproductive success is zero (González-Durán *et al.* 2018). We incorporated parameters of the depensation model into the spatial bioeconomic model of Anderson & Seijo (2010) to test two scenarios of Allee effect intensity: *i*) an unexploited *stock* and *ii*) a heavily exploited *stock*.

Methods

Given the biology of sedentary species with little or no movement, a spatial dynamic model was fitted to represent the population dynamics of a hypothetical sedentary species, in this case a sea cucumber. The model proposed by Seijo *et al.* (1994) was based on Caddy's model (1975) and was later improved by Anderson & Seijo (2010). The Allee effect was incorporated using the equation by Hilborn *et al.* (2014) and modified by González-Durán *et al.* (2018), as:

$$D = 1 - e^{-\frac{\ln(0.5)d}{q(d_0)}} + d_1 \quad \text{eq. 1}$$

Where: D is the percentage of adults contributing to spawning, d is the density of adults, q is the depensation parameter, d_0 is the maximum density, and d_1 is the offset from the origin (González-Durán *et al.* 2018). All parameters were obtained from González-Durán *et al.* (2018). Since the spatial model divides the area of distribution of the species into a grid of 25×25 (625 cells), the total spawning biomass was obtained from the sum of the adults that contribute to spawning in each grid cell. Recruitment was calculated with the Beverton & Holt (1957) equation:

$$R_t = \frac{\alpha + SSB_{t-1}}{\beta + SSB_{t-1}} \quad \text{eq. 2}$$

Where: R_t is recruitment in time t , SSB_{t-1} is the spawning stock in the previous time, α is the maximum number of recruits, and β is the spawning biomass that produce $\alpha/2$ recruitment. All the parameters for the spatial model correspond to the sea cucumber *Isostichopus badionotus* (Selenka 1867).

The spatial model represented the growth of the species by means of the von Bertalanffy equation. The equations to calculate survival, fishing mortality, biomass, catchability, selectivity, quasi-profits of the resource rent, spatial effort allocation, catch, net revenues and the number of boats, are described in detail in Anderson & Seijo (2010), see Annex 1. Other parameters included maximum age, age of sexual maturity, maximum length, Beverton & Holt recruitment parameters, initial spawning stock, area of distribution, area swept per day, initial number of vessels, average fishing

days per vessel, price, transfer cost, variable costs, fix cost, rate of discount and Smith's fleet dynamic parameter (exit-entry parameter). Model parameters are included in Annex II. The model was run under the assumption that the fishery operated in open access for a period of 25 years. The outputs analysed were total biomass, spawning biomass, recruitment, and the net present value of the resource rent obtained throughout the simulation period.

Hilborn *et al.* (2014) proposed an equation to model a depensatory impact that reflected the fraction of females that mate in different marine populations. Their model shows a monotonic relationship between density and the probability of mating, where the mating fraction can be interpreted as the probability of reproduction. According to the function, the mating fraction starts at zero, at a "very" low density (Allee threshold), and subsequently monotonically increases as the density increases. The mating fraction does not change at a constant rate, but it decreases as the density increases, until mating fraction is one at a point also called the Allee threshold. González-Durán *et al.* (2018) incorporated the depensatory function of Hilborn *et al.* (2014) in the spatial model of Seijo & Anderson (2010) and showed that the Allee effect could produce significant impacts on a sea cucumber population, even to collapse. Stoner *et al.* (2012) observed that the Allee effect in a population of queen conch (*Aliger gigas*) could be enhanced by fishing intensity. These authors compared the depensation in conch populations in a protected area (no-take zone) versus two intensely exploited areas. They observed that the effect of exploitation on the depensation model was a change in the slope of the relationship between the probability of reproduction and density resulting in a higher density required for a given probability of reproduction.

This study aims to demonstrate that depensation enhanced by fishing intensity could have a greater impact on the sea cucumber population if the population responded in a similar way to that observed by Stoner *et al.* (2012). To achieve this, the Hilborn *et al.* (2014) model was adjusted to reproduce a similar output to that observed by Stoner *et al.* (2012) where the slope of the curve was reduced by modifying the position of the depensation threshold when the probability of reproduction is one. The magnitude of the change was in accordance with that reported by Stoner *et*

al. (2012). These authors found that the magnitude of the enhanced Allee effect in the heavily exploited area caused the stock to have to increase its density by up to 67% to maintain the 50% mating probability compared to the protected area. In this study, we applied a 56% increase of density to keep the probability of reproduction success at 50% as well. This was done by adjusting the parameter q (slope of depensation model) within a range of 0.00-0.10, where 0.03 has been used for sea cucumbers (González-Durán *et al.* 2018) and where 0.10 represents a high Allee effect for invertebrates (Hilborn *et al.* 2014). The parameter d_1 was adjusted to maintain the same origin (Table 1). Therefore, the simulation experiment consisted of two effects: 1) “Unenhanced Allee effect”, where the model was run with the Allee effect function with the original parameters reported by González-Durán *et al.* (2018) and 2) “Enhanced Allee effect”, where the model

was run with the modified function as explained above to represent the Allee effect enhanced by fishing intensity.

The results were analysed from the fourth year of the simulation, as the differences in the two test scenarios became more apparent from that year. Therefore, the model outputs considered the original year four of the simulation as if it were year zero. Given that the bioeconomic model was likely to predict the collapse of the stock in both scenarios, the following experiment was carried out to determine the exact year in which it would still be possible to recover the stock. We simulated the establishment of a moratorium on the fishery one year before the population collapsed and re-ran the model. We looked at the trajectory of the total biomass and noted whether or not it would recover. If the biomass did not recover, we repeated the same procedure but stopped the fishing effort a year before. We continued like

Table 1.

Values of the parameters to simulate the displacement of the slope (q) of the depensation relationship because of the fishing pressure

Scenario	q	d_0	d_1
1) Unenhanced Allee effect	0.03	4.5 ind m ⁻²	2.12 ind m ⁻²
2) Enhanced Allee effect	0.10	4.5 ind m ⁻²	0.64 ind m ⁻²

this until we observed the recovery of the stock. When the biomass showed an upward trend (recovery signal), we ended the experiment and defined the “point of no return” (PNR) as the last year in which the biomass would collapse even if the fishing effort had stopped.

Results

An increase in the value of the slope of the Allee effect equation (q) from 0.03 to 0.10 produced a greater depensation, which translated to a lower probability of reproduction for the adult stock for

a given density (Fig. 1). At the same density, this probability was lower for the fished stock with an enhanced Allee effect than in the case of the stock with Allee effect unenhanced. For example, at a density of 0.05 individuals · m⁻², the probability of reproductive success fell from 50% to 19% (Fig. 1). Further to this, in the unenhanced Allee effect scenario, for the stock to achieve higher levels of reproductive success it required an increasingly higher level of density.

In the bioeconomic model simulations, the initial biomass was 31 013 tons and annual recruitment was above 50 million. After four years, the biomass decreased to about 19 500 tons in

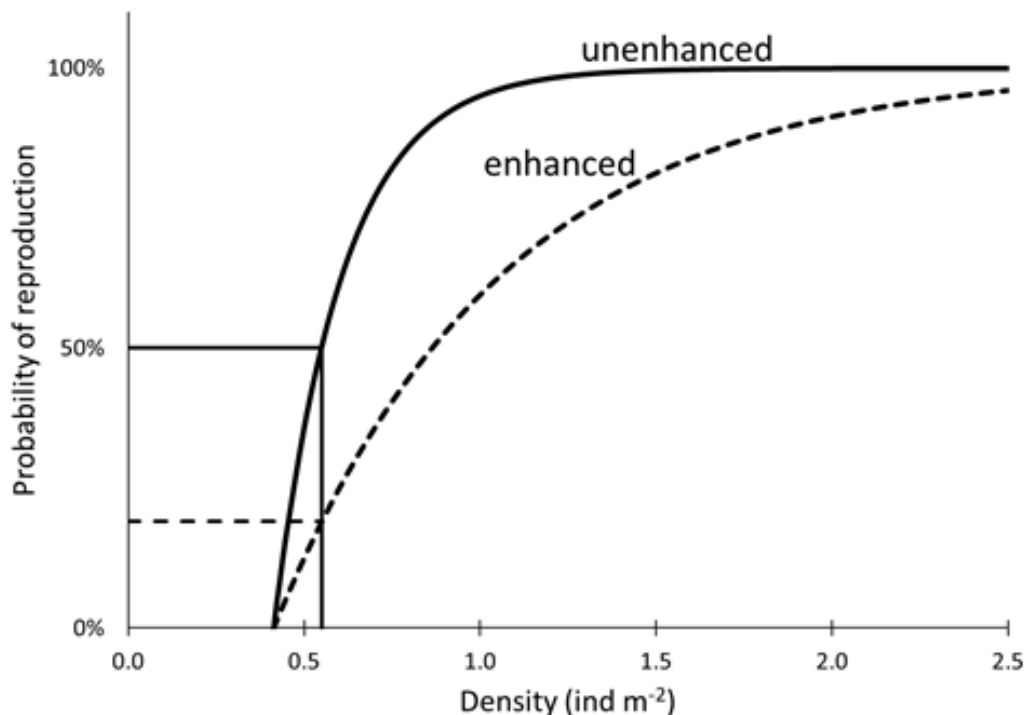


Fig. 1. Changes produced by an intensive fishing regime, “enhanced” Allee effect, on the probability of reproductive success as a function of population density vs “unenhanced” Allee effect.

both scenarios and showed downward trends in biomass and predicted stock collapse. However, the collapse occurred in 18 years under the unenhanced Allee effect scenario, whereas the stock collapsed in 13 years or five years earlier in the case of enhanced Allee effect (Fig. 2A). The behaviour of fishing effort in both scenarios was similar in the first three years of simulation; although, in the case of the enhanced Allee effect, it began to decline in year four of simulation, while in the case of the unenhanced Allee effect the decline started in year six (Fig. 2B). In year eight of the simulation, fishing effort in the unenhanced Allee effect scenario increased for three consecutive years, corresponding to a slight reduction in the decrease of biomass over the same period, before eventually decreasing again towards zero.

The Allee effect had direct and severe impacts on the spawning stocks in each scenario. In both cases, the spawning stock biomass (SSB) collapsed up to seven years earlier than the total population biomass (Fig. 2C). The SSB under enhance Allee effect due to fishing pressure collapsed four

years earlier than in the unenhanced depensation scenario. Because of the downward trend of the SSB, recruitment followed a similar decreasing pattern in both scenarios, but with a one-year lag (Fig. 2D). The catch in the two scenarios closely followed similar trends as the respective biomasses in both cases (Fig. 2E). The net present value of the resource rent for the entire simulation period was very similar in the two cases: 35.5 million dollars (MUSD) for the enhanced Allee effect, vs. 36.5 MUSD for the unenhanced depensation scenario (Fig. 2F).

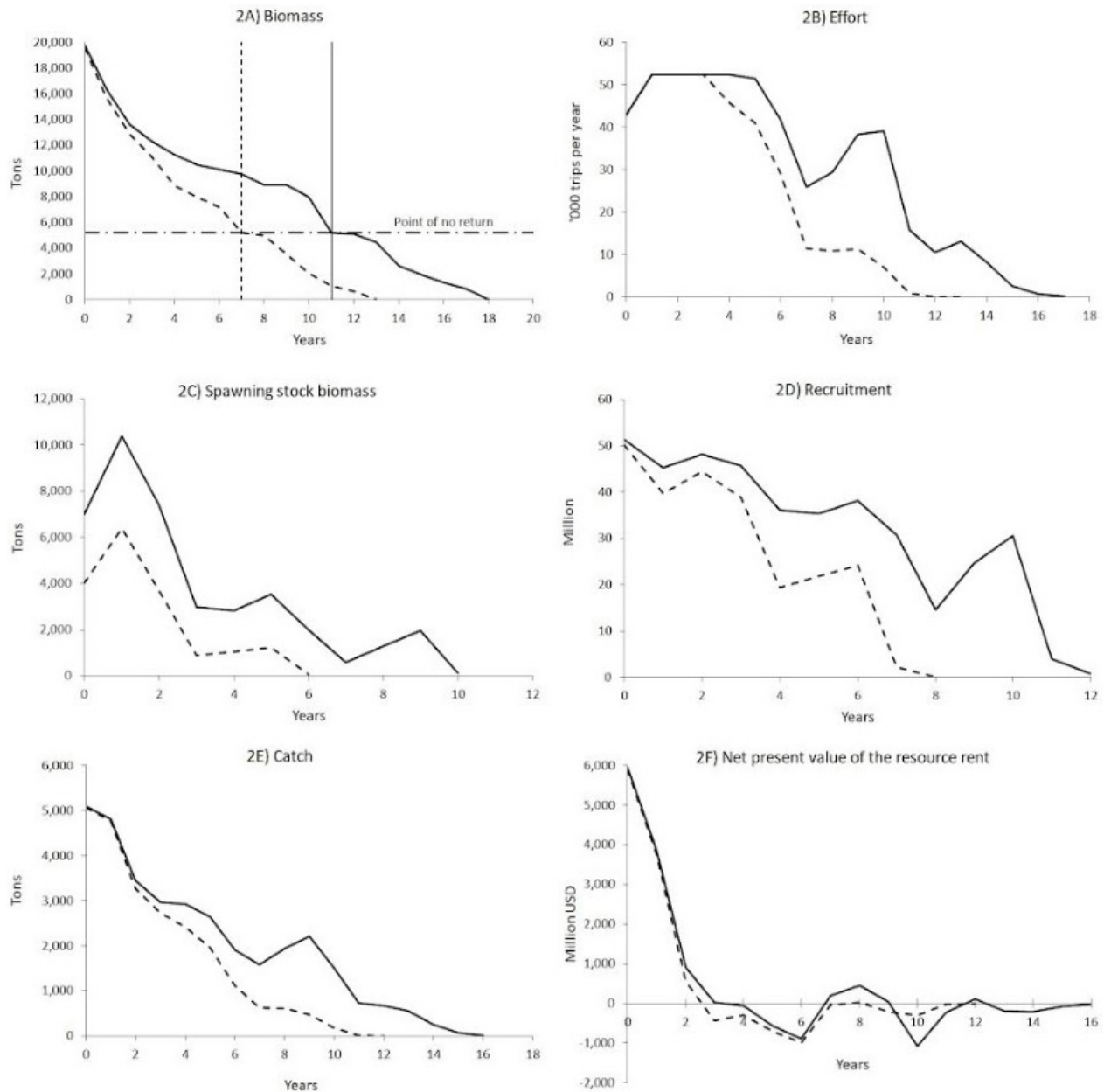


Fig. 2. Data series of the bioeconomic results of the simulation period for the two scenarios: 1) Allee effect enhanced by fishing pressure (dashed line), and 2) unenhanced Allee effect (solid line).

When fishing effort was experimentally stopped in the model to determine population recovery time, the population was no longer able to recover when fishing stopped at year five (PNR = 5), in the

case of the enhanced Allee effect (Figs. 2A and 3). When depensation was not enhanced in the model, the PNR occurred at year eight (PNR = 8) (Fig. 2A).

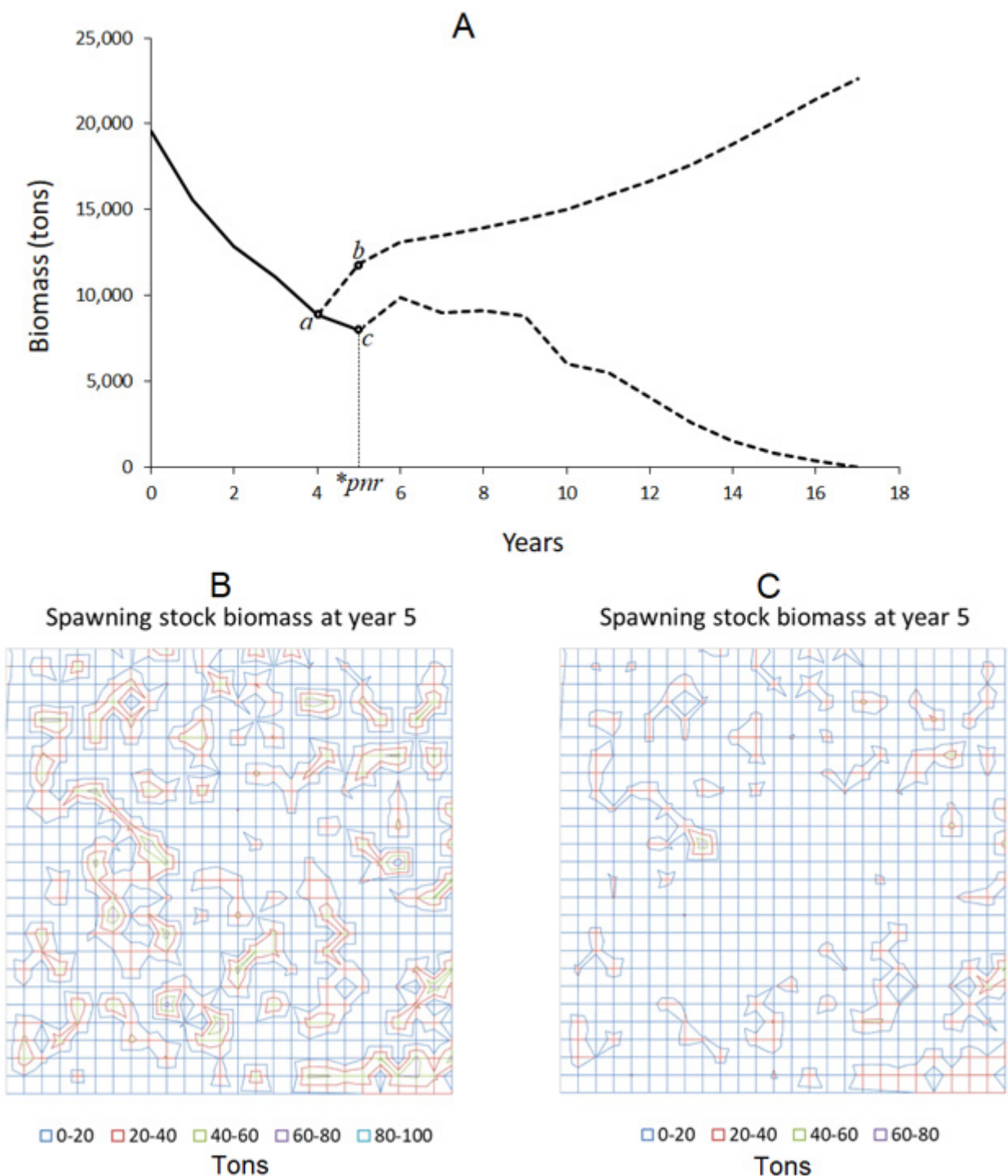


Fig. 3. A) Total biomass trajectories predicted by the model when the fishing effort was stopped in year four (dashed line starting at point *a*), and in year five (dashed line starting at point *c*). All the outputs correspond to the enhanced Allee effect scenario. B) Spatial distribution of the spawning stock biomass at year five (corresponds to point *b*) if a moratorium had been established in year four (point *a*); C) Spatial distribution of the spawning stock biomass at year five (corresponds to point *c*) if a moratorium had been established in year five ($*pnr = 5$).

Discussion

Our modelling of the low-density dynamics of a sedentary species revealed important bioeconomic consequences, particularly under open access fisheries management regimes. The intensification or enhancement of Allee effects due to fishing pressure have been demonstrated in modelling studies (Gascoigne & Lipcius 2004a) and empirical observational studies (Stoner *et al.* 2012). These have shown the effects on depensation thresholds in response to fishing mortality, or indeed catastrophic events that could result in rapid removal of sexually mature individuals. Our simulations show consistency with these studies in that, given increased fishing pressure important changes occur in the critical density thresholds (Allee and depensation thresholds) as it relates to reproductive success (mate-finding) and the critical level of fishing mortality that can be withstood by a spawning stock before a point of no return or collapse is reached. Gascoigne & Lipcius (2004a) for instance, in their model simulation, found that critical density thresholds and the strength of the Allee effect on sedentary populations experienced exponential increases as fishing pressure increased. In this study, a similar exponential change was observed as an increasingly larger density was required to maintain a given probability of reproductive success in the face of increased fishing pressure.

Our study however goes further than the aforementioned studies by showing the bioeconomic implications of the changes in critical density thresholds and the strength of the Allee effect. Stoner *et al.* (2012) demonstrated clearly that the Allee effect can be enhanced by fishing intensity, however, stopped short of demonstrating full bioeconomic effects as we have shown here. There were large differences between the performance of total biomass, the fishing effort, catch, and resource rent obtained under open access enhanced and unenhanced Allee effect scenarios. However, the most profound impact was with respect to the SSB and the subsequent recruitment, both of which showed the largest relative differences among the bioeconomic variables considered. Our simulation was that of a moderately high density-dependent species (sea cucumber *I. badionotus*) with high per capita offspring even at relatively low densities. The large difference in the SSB and recruitment in the two scenarios can be explained in that as fishing intensity is increased and the largest, most fecund individuals are removed there is less capacity for male and female gametes to find each other. This may be the case either with broadcast

spanners such as sea cucumbers and sea urchins (Gascoigne & Lipcius 2004a) or with non-broadcast spanners such as most marine gastropods (Stoner *et al.* 2012). Failure to maintain the SSB above a minimum density and abundance, coupled with uncontrolled fishing pressure can negatively impact the subsequent recruitment. Another consideration may be the spatial composition of the spawning SSB. A denser distribution may reduce the negative impact of the Allee effect compared to a more dispersed spatial distribution (González-Durán *et al.* 2018). As has been consistently concluded in the literature, a holistic and precautionary approach to sedentary species management is required. Critical depensation thresholds need to be identified and the SSB maintained above them through adaptive management.

Another important finding of our study was the point of no return (PNR) related to the threshold fishing effort beyond which the total biomass and SSB did not recover under simulated moratoria with both enhanced and unenhanced Allee effect scenarios. This point in time corresponds to the interaction of the strength of the Allee effect, the species density or abundance, and the level of exploitation all of which must be considered in management (Gascoigne & Lipcius 2004a). Our observation from the simulation that PNR under enhanced Allee effect occurred four years before the scenario under unenhanced Allee effect has important management implications. In our simulation, we identified the PNR at year five and simulated moratoria to contrast the biomass trajectories *i*) if the fishing effort was stopped at the PNR = 5 (Fig. 3C) and *ii*) if the fishing effort was stopped one year earlier in year 4 (Fig. 3B). In the former, the biomass was able to fully recover over the remaining period, while in the latter case the biomass continued a path to zero. The PNR represents the point at which exploitation drives the adult stock to such a low density that recruitment would be impaired. This was illustrated by examining the spatial distribution of the SSB in year five for both moratoria scenarios (*i.e.*, establishing a moratorium in year four and in year five, respectively), where SSB densities were much lower when fishing was stopped at the PNR (Fig. 3C). The collapse and lack of recovery of sedentary fisheries such as abalone (Karpov *et al.* 2000) and queen conch (Stoner & Appeldoorn 2021) may be the result of falling below their respective PNR. The identification of such a reference point would have been a useful tool to, at minimum, serve as a precautionary limit to avoid the irreversible collapse of the stock.

Our model also highlights the vulnerability of sedentary species with relatively high market value and incentive for exploitation. In our model, fishing effort was directed to cells with higher biomass (higher abundance with larger individuals) because of fishers maximizing short-term benefits. Consequently, reduced the abundance and density of the SSB, hindering the population's ability to reproduce and maintain the stock. If profits remained positive, there was the incentive to continue fishing, and even in the face of declining profits in the open access regime the fishing effort did not stop abruptly, but gradually. In addition, the fact that fisher behaviour is mainly based on economic incentives, rather than the status of the stock, fishing may continue even when the stock has been reduced beyond the critical density thresholds including the PNR. Given this vulnerability, a holistic and adaptive bioeconomic approach is required to implement actions on the approach reference points such as the depensation thresholds and fishing effort PNR.

Restocking and stock enhancement programmes have often been presented as a means of recovering marine stocks reduced to low density (Lipcius *et al.* 2008), however many have suffered setbacks or failure even when fishing was stopped (Stoner & Appeldoorn 2021). Among the reasons for this is the failure, in the case of the queen conch, for example, is not fully including depensation threshold reference points and how fishing affected them even before collapses occurred. Restoring sedentary marine species through artificial restocking may take years, if it is possible, and will only do so if individuals survive and reproduce. In our model, if the density did not exceed the threshold of 0.41 individuals m^{-2} in any cell, the population irretrievably disappeared as the tendency is toward local extinction. Attempts at restoration or enhancement of density-dependent sedentary species at densities below their Allee threshold are inevitably destined to fail. Our analysis and the working of Stoner *et al.* (2012) have demonstrated that these thresholds are not fixed for a given population but will change (be enhanced) if that population was subjected to fishing. Therefore, for a restocking and stock enhancement of fished species, comparatively densities may be needed due to the enhanced Allee effect. At the 50% probability of reproductive success our model considered 56% in density to maintain this level (Fig. 1), while Stoner *et al.* (2012) obtained that the change in density required to maintain the 50% probability of reproductive success was up to 70% between enhanced and unenhanced populations.

Specific studies the low-density dynamics seem a prudent compliment to every stock enhancement and restoration of sedentary species, this in addition to holistic information regarding the ecosystem including exploitation. We suggest that future research consider the source-sink configuration of sedentary resources in spatial modelling.

Conclusion

Since the first spatially explicit bioeconomic model by Caddy (1975), there has been tremendous development in the modelling of sedentary species including Seijo *et al.* (1994), Anderson & Seijo (2010), and others who have built upon the strong foundation laid by Caddy. The utility and versatility of this model have allowed us to incorporate other important aspects of sedentary species such as the Allee effect through the depensation model proposed by Hilborn *et al.* (2014). Our results allow for a deeper understanding of the intensification effect of fishing effort on the Allee effect and the spatial bioeconomic implications, further broadening our understanding of the Allee effect phenomenon in sedentary species given their patchy distribution and their gregarious behaviour. Enhanced Allee effect due to fishing effort can occur over different spatial scales increasing the risk of stock collapse in short time if not considered in management strategies. In addition, for stocks already driven to low densities, enhanced Allee effect can lead to failures of stock restoration and enhancement efforts as such stocks may require exponentially higher densities to recover relative to their unenhanced Allee effect scenario. In this study, we also defined a point of no return at which exploitation drives the spawning stock to such a low density that recruitment is impaired, and the stock did not recover even when fishing had stopped. Given this set of phenomena, the best course of action for managing sedentary species subject to exploitation is to maintain spawning stocks above the critical depensation thresholds and for fishing effort to be above the PNR limit reference point. This inevitably will require more studies that identify and quantify spawning stocks at different spatial scales and how they are affected by depensation and exploitation.

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Annex I. Summary of equations used in the spatial bioeconomic model

Equation	Description	Unit
$\frac{dN^{i,s}}{dt} = -(F^{i,s,t} + M)N^{i,s,t}$	Survival of the cohort for site	individuals
$F^{i,s,t} = E^{s,t} q^i$	Fishing mortality	rate
$W_{i,t,s} = aL_{i,t,s}^b$	Length-weight relationship	g
$X^{i,s,t} = N^{i,s,t} \cdot W^{i,s,t}$	Biomass of the cohort, at time and site	tons
$X_{t,s} = \sum_{i=1}^{i=10} X_{i,t,s}$	Total biomass	tons
$q_t = -\log \left[1 - \frac{a}{A} \right]$	Catchability coefficient (Baranov 1918)	–
$SEL^{i,s,t} = 1 + e^{(S_1 - S_2 L t)}$	Selectivity (Sparre & Venema 1998)	–
$X_{t,s} = \frac{quasi\pi_{S,t}}{\sum quasi\pi_{S,t}} V_{S,t} f d$	Fishing effort (Seijo <i>et al.</i> 1994)	Fishing trips
$quasi\pi_{S,t} = p_{Y_{S,t}} - C_{S,t}$	Quasi-profits per boat (Seijo <i>et al.</i> 1994)	USD
$C_{s,t} = \frac{\left(\left[\frac{D_s}{v} \right] c_1 + \left[L - \frac{D_s}{v} \right] c_2 \right)}{L}$	Cost per fishing trip (Anderson 2002)	USD
$Y_t = \sum_s \sum_{i=1} p X_{i,t} \cdot \left(\frac{F_{i,t}}{F_{i,t} + M} \cdot (1 - e^{-F_{i,t} + M}) \right)$	Total catch (adapted from Baranov 1918)	tons
$\pi_t = \sum_s (p Y_{s,t} - C_{s,t} E_{s,t}) - FC \cdot V_t$	Net revenues of the fleet	USD
$V_{t+1} = V_t + \phi \left[\sum_s (p Y_{s,t} - C_{s,t}) - FC V_t \right]$	Fleet dynamic (Smith 1969)	Boats
$SSB_{s,t} = \sum_{i=2}^{mage} N_{i,s,t} w_i$	Spawning stock biomass	tons

Where: *i* is the population cohort located in site *s* in time *t*.

Annex II. Parameters used in the spatial bioeconomic model

Parameter	Symbol	Value	Unit
Maximum age ^a	mage	10	year
Age of sexual maturity ^a	-	2	year
Maximum length ^a	L_{∞}	31.6	cm
Maximum weight ^a	W_{∞}	1 110	g
Beverton & Holt recruitment parameter ^b	α	55 724 807	individual
Beverton & Holt recruitment parameter ^b	β	1 618	tons
Length weight parameter ^a	β_1	0.27	-
Natural mortality coefficient ^b	M	0.58	year ⁻¹
Initial spawning stock ^c	X_0	8 924	tons
Area of distribution ^c	A	1 702	km ²
Area swept per day ^b	-	6.9	km ²
Number of geographic cells ^b	-	625	cell
Area of cell ^b	-	2.72	km ²
Initial number of vessels ^c	-	1	Vessel
Avg. number of fishing days per vessel ^c	-	76	Days/year
Price range ^b	P	2 000-3 500	USD/kg
Unit transfer cost ^b	C_1	75	USD/day
Other variable costs ^b	C_2	40	USD/day
Fix cost ^b	FC	860	USD/year
Rate of discount ^b	δ	0.05	year ⁻¹
Exit/entry parameter ^b	ϕ	0.00004	Boat/USD

Sources: a. Poot-Salazar *et al.* (2014); b. Hernández-Flores *et al.* (2018); c. Hernández-Flores *et al.* (2015).